Behavioural ecology at the spatial-social interface

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## Abstract

Spatial and social behaviour are fundamental aspects of an animal’s biology, and the social and spatial environments are indelibly linked through mutual causes and shared consequences. Behavioural variation at the “spatial-social interface”, which we define as the intersection of social and spatial aspects of individuals’ phenotypes and environments, has implications for ecological and evolutionary processes including pathogen transmission, population dynamics, and the evolution of social systems. Traditionally, the spatial and social dimensions of animal biology have been studied separately despite many conceptual and practical similarities. The lack of shared vocabulary or direct alignment of analogous concepts has prevented unification of social and spatial behaviour, which diminishes the potential for synthesis, reduces the power of integrated analyses, and results in missed opportunities to test both spatial and social hypotheses. We bridge the spatial-social interface by outlining a foundation of shared theory, vocabulary, and methods. We discuss the integration of spatial and social behaviour, identify shared concepts and approaches, and discuss how these concepts can be integrated to identify and test questions at the spatial-social interface.

**Keywords:** behavioural ecology, collective movement, ecological niche, movement ecology, social environment, social niche, social phenotype, social network, spatial environment, spatial phenotype.

CONTENTS

1. Introduction
2. Relationships between social and spatial processes
	1. Social environment and spatial environment
		1. Mechanisms and consequences
		2. Key next steps and testable hypotheses
	2. Social phenotype and spatial phenotype
		1. Mechanisms and consequences
		2. Key next steps and testable hypotheses
	3. Social phenotype and spatial environment
		1. Mechanisms and consequences
		2. Key next steps and testable hypotheses
	4. Spatial phenotype and social environment
		1. Mechanisms and consequences
		2. Key next steps and testable hypotheses
3. Shared concepts and terminology
	1. Ecological and social niche specialization
	2. Graph theory and the use of networks to describe social and spatial processes
	3. Ideal free distribution and density-dependent habitat selection
	4. Optimal group size
	5. Geometry of the selfish herd
4. Movement as a mechanism for linking social and spatial behaviour
	1. Internal state
	2. Motion capacity
	3. Navigational capacity
5. Conclusion
6. References

## I. Introduction

The environment that an animal experiences both shapes and is shaped by its spatial and social behaviour. Fundamentally, spatial and social behaviours are influenced by similar mechanistic drivers like predation [(Creel *et al.* 2014)](https://www.zotero.org/google-docs/?HWelMS), foraging [(Giraldeau & Dubois 2008)](https://www.zotero.org/google-docs/?f55WpS), mating [(Maldonado-Chaparro *et al.* 2018)](https://www.zotero.org/google-docs/?9oPEhy), or parasitism [(Albery *et al.* 2020, 2021a)](https://www.zotero.org/google-docs/?7KZ5SU). For example, animals socially aggregate to share vigilance for predators, e.g., through the “many eyes” effect [(Lima 1995)](https://www.zotero.org/google-docs/?0PA6w0) or confusion effect [(Krause & Godin 1995)](https://www.zotero.org/google-docs/?yaoa1v). Meanwhile, space use can be shaped by the spatial distribution of predation risk, i.e., the “landscape of fear” [(Brown *et al.* 1999; Peers *et al.* 2018)](https://www.zotero.org/google-docs/?NUZsda). Additionally, spatial and social behaviours can influence each other [(Spiegel *et al.* 2016; Webber & Vander Wal 2018)](https://www.zotero.org/google-docs/?Qtu4yC). The spatial distribution of resources shapes the opportunity to be in proximity to, and socially interact with, conspecifics, while social information about food sources can shape space use decisions [(Fletcher & Sieving 2010; Firth & Sheldon 2016; Spiegel & Crofoot 2016)](https://www.zotero.org/google-docs/?eTZz6i). Finally, social and spatial behaviours can have shared consequences for ecological processes. For example, spatial behaviours, such as habitat selection, are fundamental for resource acquisition [(Duparc *et al.* 2019)](https://www.zotero.org/google-docs/?1NDA5i), and animals often form social groups to gain access to certain resources or to improve foraging efficiency [(Glück 1987; Silk 2007; Cantor *et al.* 2020)](https://www.zotero.org/google-docs/?WJdHJa), both of which can alter population dynamics. Due to these pervasive interdependencies, many ecological studies benefit from considering both spatial and social behaviours in tandem. Yet, despite being strongly interconnected through their origins, interactions, and emergent implications, spatial and social processes have predominantly been considered independently.

Studies that incorporate both spatial and social components are beginning to emerge and span diverse fields, including movement ecology [(Jesmer *et al.* 2018; Webber *et al.* 2021)](https://www.zotero.org/google-docs/?Ya9ePJ), landscape ecology [(Armansin *et al.* 2020)](https://www.zotero.org/google-docs/?AAwihq), disease ecology [(Albery *et al.* 2021a)](https://www.zotero.org/google-docs/?7ywEoG), and evolutionary ecology [(Formica *et al.* 2021)](https://www.zotero.org/google-docs/?5I6H72). Recent integration of concepts from spatial and social behavioural ecology can be attributed to advances in biologging technologies, which have historically informed spatial dimensions of behaviour [(Kays *et al.* 2015)](https://www.zotero.org/google-docs/?jj83hL), but are also now used to characterize diverse social dimensions of behaviour [(Smith & Pinter‐Wollman 2020)](https://www.zotero.org/google-docs/?m8TBU4). Yet despite their utility and increasing accessibility, core concepts at the spatial-social interface lack formal integration. We suggest three main causes for this persistent disconnect. 1) Spatial and social behaviours are often examined separately, and by different teams of researchers, instead of in a unified framework and through collaboration. 2) Semantic and methodological gaps impede the ability of practitioners to identify points for analogy or synergy that would improve unification. 3) Spatial and social behaviour are often quantified and studied at different scales that preclude formal integration.

Bridging theory and methods from social and spatial behaviour has several benefits. First, uncovering how and why spatial and social behaviours influence one another in additive or synergistic ways; second, sharing useful concepts and theory across disciplines; third, improving accuracy, breadth, and reliability of models of behaviour by incorporating drivers from one field into the other. To improve the integration of spatial and social behaviour, we present a synthetic framework that integrates theory and methods from these two fields. Our framework has four objectives:

1. We develop conceptual links between social and spatial behaviours (Figure 1; Table 1) and propose a series of testable hypotheses at the spatial-social interface (Table 2).
2. We identify shared concepts and vocabulary (Table 1; Glossary).
3. We discuss existing areas of research in which social and spatial behaviour have been implicitly and explicitly integrated (Section III).
4. We highlight foundational ecological concepts in which the integration of social and spatial behaviours remains implicit. We extend our conceptual framework to outline how animal movement, which is intertwined with spatial and social behaviour, can be used to interrogate the causes and consequences of the spatial-social interface (Figure 2).

II. Relationships between social and spatial processes

We consider the spatial-social interface to operate as four interconnected components (Figure 1). We define the **spatial-social interface** as the proximate and ultimate interactions between social and spatial phenotypes and environments. In the framework, individual **social phenotypes** and the **social environment** are linked to individual **spatial phenotypes** and to the underlying **spatial environment**. A phenotype is a suite of characteristics that reflect underlying interactions between an individual’s genotype and its environment. For a phenotype to evolve, it must differ between individuals, have some degree of within-individual repeatability and heritability, and drive variation in fitness. We assume that social and spatial phenotypes meet these criteria, but for many phenotypic traits direct tests of these assumptions may be necessary. An environment is a set of circumstances characterized by risks, resources, and conditions [(Manly *et al.* 2002; Matthiopoulos *et al.* 2020)](https://www.zotero.org/google-docs/?NlhaDh) in which an animal lives (Table 1; Glossary). The fitness that the environment imparts can differ among individuals: for example, individuals living in the same geographic area may vary in their thermal optima or dominance rank, leading to different fitness outcomes under identical conditions. This variation may produce different optimal habitat or social group configurations for different individuals.

An individual’s **spatial environment** involves two components: geographic and environmental space [(Van Moorter *et al.* 2016)](https://www.zotero.org/google-docs/?H6JvTa). Geographic space concerns the size and location of animals’ home ranges and the physical attributes of their ranges in two- or three-dimensional space [(Moorcroft 2012)](https://www.zotero.org/google-docs/?4p3hzu). Environmental space comprises abiotic and biotic factors like climatic conditions (e.g., temperature or humidity), risks (e.g., predators), resources (e.g., mates or food) and their spatial distributions [(Manly *et al.* 2002; Matthiopoulos *et al.* 2020)](https://www.zotero.org/google-docs/?zLyjio). An individual’s fitness depends in part on its spatial environment, and the scale of the spatial environment is dependent on the ability of an animal to move: the fitness of long-distance migrants may depend on climatic conditions over whole wintering and breeding grounds, while fitness for small rodents more likely reflects local weather conditions. Animals have physiological and energetic requirements that must be met by surrounding biotic and abiotic conditions. Thus, environmental space limits geographic ranges to locations within an individual’s ecological niche. Together, available geographic and environmental space dictate accessibility and the suite of resources, risks, and conditions that the animal must face to survive, grow, and reproduce.

The **social environment** is conventionally defined as the nature, quality, and patterning of relationships among members of a group or population, including group size, group composition, fission-fusion dynamics, and the social interactions among group members (following Hinde [(1976)](https://www.zotero.org/google-docs/?v5jDcj); Table 1). The social environment can differ among individuals within the same group, for example when different individuals have different interactions with one another. In contrast, the spatial environment experienced by a group at a given time is effectively the same for all individuals in the group.

An individual’s **spatial phenotype** incorporates aspects of space use and is defined as the movement to, from, and within geographic and environmental space (i.e., the spatial environment). Within the context of habitat selection, spatial phenotypes are processes whereby an individual uses a habitat component disproportionately more than that component’s availability [(Manly *et al.* 2002; Matthiopoulos *et al.* 2020)](https://www.zotero.org/google-docs/?bWfpEG). Examples of spatial phenotypes include home range size [(Schirmer *et al.* 2019)](https://www.zotero.org/google-docs/?TXKFGa), habitat selection [(Leclerc *et al.* 2016)](https://www.zotero.org/google-docs/?iy319s), environmental niche specialization [(Sheppard *et al.* 2018; Carlson *et al.* 2021)](https://www.zotero.org/google-docs/?FIo4fA), foraging search performance [(Webber *et al.* 2020)](https://www.zotero.org/google-docs/?KTeJbj), and daily movement distances [(Hertel *et al.* 2021)](https://www.zotero.org/google-docs/?4mKsL8), all of which may exhibit consistent within- and among-individual variation. Spatial phenotypes may also be learned [(Nielsen *et al.* 2013)](https://www.zotero.org/google-docs/?1LNjkD) or related to natal habitat preference [(Stamps *et al.* 2009)](https://www.zotero.org/google-docs/?t1jhqA).

Meanwhile, an individual’s **social phenotype** is the extent to which it interacts with conspecifics, and occasionally heterospecifics [(Hillemann *et al.* 2019)](https://www.zotero.org/google-docs/?JEclrJ), through mating, grooming, or other types of social interactions. An individual’s social phenotype is therefore a reflection of it’s position in a society. For example, mating strategies [(Fisher *et al.* 2016)](https://www.zotero.org/google-docs/?5ZIC6i), aggression level [(Kilgour *et al.* 2018)](https://www.zotero.org/google-docs/?WpR1hP), and cooperative behaviour [(Dakin & Ryder 2018)](https://www.zotero.org/google-docs/?r0S6Fb) are quantifiable social phenotypes, all of which are impacted by the social environment and some by the spatial environment.

Despite a lack of formal integration, there is implicit integration embedded in the theory and methods used regularly to study social and spatial behaviour. For example, social association is often defined using spatial thresholds [(Franks *et al.* 2010; Haddadi *et al.* 2011)](https://www.zotero.org/google-docs/?ddnO55) and spatial sampling designs can be informed by social structure [(Mladenoff *et al.* 1999)](https://www.zotero.org/google-docs/?cULR5B). Among the four combinations of phenotypes and environments, there are six possible pairwise interactions, each with unique implications for an animal’s ecology (Figure 1). In this section, we highlight underlying mechanisms and ecological and evolutionary consequences and identify potential areas of future research and accompanying testable hypotheses for each link (Table 2).

### (1) Social environment and spatial environment

1. *Mechanisms and consequences*

The spatial environment provides the geographic space within which animals aggregate, interact, and form the social environment. Therefore, the spatial environment should affect the social environment on the basis of first principles alone: the ideal gas law predicts that individuals in a high-density population will be more socially connected simply by chance compared to individuals in lower-density populations [(Hutchinson & Waser 2007; Sanchez & Hudgens 2015)](https://www.zotero.org/google-docs/?rOF93l). Animals’ propensity to form groups may depend on habitat [(Barja & Rosellini 2008)](https://www.zotero.org/google-docs/?qq31Bm), time of year [(Peignier *et al.* 2019)](https://www.zotero.org/google-docs/?f4O8Uv), or physical constraints [(Pinter-Wollman *et al.* 2018)](https://www.zotero.org/google-docs/?mbBVrf). For example, wildfires alter habitat and resource availability in the spatial environment of red-backed fairy wrens (*Malurus melanocephalus*), with social connectivity increasing as a result [(Lantz & Karubian 2017)](https://www.zotero.org/google-docs/?z8QCQb). Similarly, the collective (i.e., social) behaviour of harvester ants is influenced by the spatial structure of the nest [(Pinter-Wollman 2015b, a)](https://www.zotero.org/google-docs/?Gcf5F4), and the available resources in the spatial environment can shape the social environment through habitat specialization [(Janson & Boinski 1992; Cantor & Farine 2018; Sheppard *et al.* 2021)](https://www.zotero.org/google-docs/?3RBmka).

Reciprocally, the social environment can determine the spatial environment through effects of population density, resource depletion, habitat selection, dispersal, or direct environmental engineering. For example, the **environmental engineering hypothesis** (Table 2) predicts that the group composition of ants with polymorphic workers (*Veromessor pregandei*) determines the structure of the nests they construct [(Kwapich *et al.* 2018)](https://www.zotero.org/google-docs/?tl4wCd). These nests form the spatial environment in which the ants live and function as a colony. In addition, herbivore movements can determine seed dispersal patterns [(Nield *et al.* 2020)](https://www.zotero.org/google-docs/?dsuIOO) or food availability [(Janson & Boinski 1992)](https://www.zotero.org/google-docs/?qawetY), which drives the subsequent distribution of plants and food in the spatial environment. Density-dependent habitat selection can determine where individuals settle and therefore the spatial environment. For example, Allee effects, which are positive relationships between individual fitness and population size or density [(Stephens *et al.* 1999)](https://www.zotero.org/google-docs/?AJbt6m), can influence the speed of species invasion into new habitats, thus influencing the spatial environment in which individuals encounter one another [(Taylor & Hastings 2005)](https://www.zotero.org/google-docs/?5Mh1bO). In some cases it is clear that temporal changes in the spatial environment lead to changes in the social environment (e.g., seasonal cycles), but at most scales whether, how, and when this principle operates is still poorly known.

Both the spatial and social environments are composed of constant and time-varying components. For example, in temperate environments, the emergence of plants each spring can be quantified as the normalized difference vegetation index (NDVI), an index which uses remote sensing to quantify live green vegetation in the spatial environment [(Pettorelli *et al.* 2005)](https://www.zotero.org/google-docs/?mt7lNk). NDVI varies at a given location through time, while other spatial factors, like elevation, remain constant. Meanwhile, in the social environment, mate availability varies through time – e.g., as ranks and female estrus status change [(Hogg 1988)](https://www.zotero.org/google-docs/?VYt6ee) – even when kinship is constant within a given group. Temporal fluctuations in the spatial environment (e.g., food resources) may generate fluctuations in the social environment (e.g., aggregation size [(Sapolsky 1986; Brown & Brown 2014)](https://www.zotero.org/google-docs/?Dzj7pb)), and *vice versa*. For example, pulsed births in some species lead to population-wide shifts in habitat selection while neonates are young and vulnerable to predation [(Ims 1990)](https://www.zotero.org/google-docs/?1DSZRP). In some cases, the social environment may vary spatially or temporally, e.g., influenced by spatial or temporal variation in resource availability [(Bonnell *et al.* 2019)](https://www.zotero.org/google-docs/?uo5JKp).

1. *Key next steps and testable hypotheses*

An understanding of the mechanisms driving relationships between social and spatial environments requires comparable descriptions of animal social structure – ideally along with life history, phenology, or physiology – across a range of systems and spatial environments. Most pressingly, there are relatively few known scenarios in which the social environment shapes the spatial environment. The roles an individual’s (or population’s) social and ecological niches play in the feedback between the two types of environments remain under-studied. Fitness associated with a given social environment may depend on the spatial environment, and *vice versa*. For example, some species have spatially distinct mating grounds and the spatial distribution of the social environment may be determined by the physical locations of mating sites [(Maldonado-Chaparro *et al.* 2018)](https://www.zotero.org/google-docs/?VnFLQM). The interactive effects of the spatial and social environments on fitness are an important area for future investigation, particularly where they complicate inference of either environment’s selective influence.

Finally, the spatial environment may drive aspects of the social environment from the bottom up by shaping genetic relationships among individuals, groups, and populations. For example, spatially (and therefore socially) connected groups have higher inter-group relatedness and gene flow [(Armansin *et al.* 2020)](https://www.zotero.org/google-docs/?daXrTY). Within the context of the genetic relationships among potentially spatially constrained groups, the **social resistance hypothesis** (Table 2) predicts that genetic relatedness and gene flow could be influenced by the relationship between the social and spatial environments [(Armansin *et al.* 2020)](https://www.zotero.org/google-docs/?LFt1tk). The effects of social and spatial environments on genetic interrelationships present opportunities to test hypotheses about their effects on fitness and consequences for evolution of spatial and social behaviours.

### (2) Social phenotype and spatial phenotype

1. *Mechanisms and consequences*

Spatial and social phenotypes are related through a variety of mechanisms, and their covariance is relatively well studied across a wide range of systems. A range of complex mechanisms underlie covariance between social and spatial phenotypes. For example, the location where individuals forage (a spatial behaviour) can be socially learned [(Page & Ryan 2006; Mazur & Seher 2008; Rapaport & Brown 2008; Keynan *et al.* 2015)](https://www.zotero.org/google-docs/?HKFciS), and individuals with large home ranges may encounter more social partners [(Albery *et al.* 2021b)](https://www.zotero.org/google-docs/?qhmdSy). Conversely, territorial species may have restricted social encounters because they are spatially constrained by the location and size of their own territories and others territories [(Wagner *et al.* 2008)](https://www.zotero.org/google-docs/?KHgcBr). Spatial phenotypes incorporate aspects of shared preference for a given site or territorial neighbours. Consequently, social phenotypes can be highly spatially autocorrelated.

An individual’s social and spatial phenotypes may be correlated because the spatial phenotype determines the way an individual engages with its environment and the social phenotype is influenced by these environmental gradients. Additionally, relationships between social and spatial phenotypes may be produced by shared intrinsic drivers, like reproductive state, that affect both [(Saveer *et al.* 2012)](https://www.zotero.org/google-docs/?oAg5EU). Importantly, such apparent links may arise spuriously due to methodological approaches. For example, spatial thresholds are commonly used to infer social interactions, with varying validity and success [(Castles *et al.* 2014; Farine 2015; Gilbertson *et al.* 2021)](https://www.zotero.org/google-docs/?BLsn2C). More generally, social network position is one measure of an individual’s social phenotype, but both spatial phenotypes and environments play a role in driving social network position. As such, the interpretation of social position needs to be carefully validated against known spatial phenotypes, spatiotemporal confounding variables, and null models [(Pinter-Wollman *et al.* 2014; Spiegel *et al.* 2016; Farine 2017; Albery *et al.* 2021b; Hobson *et al.* 2021)](https://www.zotero.org/google-docs/?F7nmGr).

Covariance between social and spatial phenotypes may be interpreted within the context of consistent individual differences in behaviour (i.e., animal personality). Empirical evidence supports the idea of repeatability in social phenotypes through space and time [(Wolf & Krause 2014; Ward & Webster 2016)](https://www.zotero.org/google-docs/?hZYMFg): even in systems with relatively unstable social groups, individuals tend to repeatedly interact and associate with the same individuals [(Aplin *et al.* 2015; Strickland & Frère 2018)](https://www.zotero.org/google-docs/?0m8DJK). Similarly, animals display consistent individual differences in spatial phenotypes [(Leclerc *et al.* 2016; Webber *et al.* 2020; Hertel *et al.* 2021; Stuber *et al.* 2022)](https://www.zotero.org/google-docs/?hwPEpN). The similarities and differences in the magnitude of repeatability in spatial and social phenotypes could influence the degree to which they covary. Furthermore, consistent individual differences in spatial and social phenotypes may be linked to traditional animal personality traits [(Wolf & Krause 2014; Spiegel *et al.* 2017)](https://www.zotero.org/google-docs/?wPLN7w), such as exploration and boldness [(Nomakuchi *et al.* 2009; Minderman *et al.* 2010; Aplin *et al.* 2013, 2015; McCowan *et al.* 2015; Spiegel *et al.* 2017)](https://www.zotero.org/google-docs/?HvYdBj). Suites of traits that are correlated across time and contexts are known as behavioural syndromes [(Sih *et al.* 2004)](https://www.zotero.org/google-docs/?fMKZ3U) and in the case of the spatial-social interface, correlations between these two types of phenotypes could be interpreted as a socio-spatial behavioural syndrome [(Webber & Vander Wal 2018)](https://www.zotero.org/google-docs/?S8HEvf).

1. *Key next steps and testable hypotheses*

While spatial and social phenotypes are often known to covary, the causative mechanisms underlying these links – and their ecological consequences – remain an important research priority. Spatial and social phenotypes may covary when the spatial phenotype that optimizes fitness of one social phenotype is not optimal for a different social phenotype. The strength of the covariance will then increase with increasing divergence in the fitness outcomes across spatial and social phenotype combinations. However, there are relatively few examples of this phenomenon, and the mechanisms underpinning and modifying this covariance remain unknown. For example, the correlation between social and spatial phenotypes could change according to food availability, being either more or less correlated in high-resource areas. Examining how the effects of social phenotypes on fitness are modulated by spatial phenotypes is an important topic for future investigation.

There are established but infrequently tested hypotheses for the mechanisms that underlie the covariance between spatial and social phenotypes (Table 2). For example, the **pace-of-life syndrome hypothesis** (Table 2) predicts that aspects of physiology (e.g., hormone production) or life-history (e.g., senescence) will shape variation in spatial and social phenotypes [(Silk & Hodgson 2021)](https://www.zotero.org/google-docs/?sqVD0M). Similarly, the **habitat matching hypothesis** (Table 2) predicts that less-social individuals will settle in low density sites and more-social individuals will settle in high density sites, while fitness outcomes for individuals in each habitat are predicted to be approximately equal [(Fagen 1987; Morris 1994)](https://www.zotero.org/google-docs/?r3JSG4). In many cases, low quality habitats host lower population densities, and thus will require both more movement to encounter resources while supporting individuals that are less social, which could result in covariance between spatial and social phenotypes [(Cote & Clobert 2007; Spiegel *et al.* 2015)](https://www.zotero.org/google-docs/?cBMo3V). Similarly, habitats with high quality, but clumped, resources are predicted to select for more social individuals and reduced local movement since these high quality patches are dense populations [(Spiegel *et al.* 2017)](https://www.zotero.org/google-docs/?dSAL6m). Validating or rejecting the predictions of these hypotheses will require regular joint examination of spatial and social phenotypes across ecological systems.

### (3) Social phenotype and spatial environment

1. *Mechanisms and consequences*

The expression, costs, and benefits of social phenotypes depend on variation in the resources, risks, and climatic conditions within the spatial environment. For example, animals may form larger groups in risky habitats [(Lima 1995)](https://www.zotero.org/google-docs/?H5jkIO), huddle to save energy through social thermoregulation [(Gilbert *et al.* 2010)](https://www.zotero.org/google-docs/?v7IVus), and use social cues to find important resources [(Harel *et al.* 2017)](https://www.zotero.org/google-docs/?I9alE1). The **information centre hypothesis** (Table 2) predicts that colonial living is advantageous because individuals that lack personal information about resources benefit from following cues from informed associates, whom they follow to previously visited resources [(Ward & Zahavi 1973)](https://www.zotero.org/google-docs/?GyGcXd). While resources, risks, and climatic conditions are spatiotemporally dynamic, other aspects of the spatial environment (e.g., topographic features) can generally be considered static within the lifetime of an individual. Some habitat features (e.g., water holes or dense vegetation) may promote or inhibit social interactions among animals [(Leu *et al.* 2016)](https://www.zotero.org/google-docs/?xl8IxB). Certain landscape features, such as barriers formed by rivers or mountains, may result in insular social communities [(Armansin *et al.* 2020)](https://www.zotero.org/google-docs/?2SbGm1) and influence collective movement [(Pinter-Wollman 2015a; Strandburg-Peshkin *et al.* 2017; Pinter-Wollman *et al.* 2018)](https://www.zotero.org/google-docs/?7wUUHo). Social phenotypes can therefore emerge from both dynamic and static aspects of the spatial environment, and both individuals and groups may match their social phenotypes to environmental conditions.

Phenotypic plasticity is the ability of a genotype to produce distinct phenotypes when exposed to different environments over time [(Pigliucci 2005)](https://www.zotero.org/google-docs/?l48YGJ), and social phenotypes often demonstrate such plasticity. For example, social ties in guppy social networks (*Poecilia reticulata*) diminish in strength as predation pressure declines [(Kelley *et al.* 2011)](https://www.zotero.org/google-docs/?A91uiy). Similarly, individuals often express more competitive social phenotypes in higher-quality habitats (for a review see [(Fokkema *et al.* 2021)](https://www.zotero.org/google-docs/?eY8WiC)). Phenotypic plasticity is adaptive when animals can match their phenotype to environmental conditions and maintain high performance across a large environmental gradient, but plasticity may be costly (e.g., metabolically) and is therefore predicted to vary in direction and magnitude [(Mathot *et al.* 2012)](https://www.zotero.org/google-docs/?b9VlWf). As such, behavioural reaction norms (see Glossary), which we consider here as changes in social behaviour in response to changes in the spatial environment, may themselves differ across environments. For example, an individual may change its number of contacts in response to a stimulus in one environment, but not in another. Importantly, certain individuals might express this plasticity, and others might not.

Reciprocally, social phenotypes can influence the spatial environment. For example, large social aggregations may deposit nutrients via feces, urine, or other bodily excreta in a given area, elevating its nutrient quality [(Ellis-Soto *et al.* 2021)](https://www.zotero.org/google-docs/?5sgFck). Social groups that build dens or nests may improve the environment for other species: for example, yellow-spotted monitor lizards (*Varanus panoptes*) dig nesting burrows that provide refugia, feeding, and nesting habitat for other burrowing species [(Doody *et al.* 2021)](https://www.zotero.org/google-docs/?sLCx15). Such nests can influence both nutrients in the soil and vegetation structure through seed dispersal; for example, the nests of harvester ants and termites change the nitrogen composition of the soil, which facilitates the growth of plants in the environment [(Bonachela *et al.* 2015; Farji-Brener & Werenkraut 2017)](https://www.zotero.org/google-docs/?hkj0Hg).

1. *Key next steps and testable hypotheses*

The relationship between social phenotypes and the spatial environment fits well within the existing theoretical and methodological frameworks used to test **the social reaction norm hypothesis** [(Martin & Jaeggi 2021; Strickland *et al.* 2021)](https://www.zotero.org/google-docs/?w0agf6). Examining how social phenotypes change as a function of environmental features (e.g., risks, resources, and conditions) may reveal the causes and consequences of among-individual differences in social plasticity [(Stamps *et al.* 2012; Piza-Roca *et al.* 2018; Strickland *et al.* 2018; Strickland & Frère 2019)](https://www.zotero.org/google-docs/?80AaPM). Similarly, given that social phenotypes differ consistently among individuals [(O’Brien *et al.* 2018)](https://www.zotero.org/google-docs/?W6452x), can be heritable [(Wice & Saltz 2021)](https://www.zotero.org/google-docs/?tNViiW), and change as a function of the spatial environment (see above), an important next step is to assess the potential for the spatial environment to select for certain social phenotypes [(Formica *et al.* 2021; Vander Wal 2021)](https://www.zotero.org/google-docs/?md0m2z).

Uncovering the role of social phenotypes in shaping the configuration of the spatial environment will help interrogate dynamic feedbacks between social and spatial processes [(Pinter-Wollman 2015a; He *et al.* 2019)](https://www.zotero.org/google-docs/?NJZvcN). The sociality of ecosystem engineers may affect the level to which they alter the spatial environment [(Doody *et al.* 2021)](https://www.zotero.org/google-docs/?FlTGpn), while environmental conditions may impact individuals’ tendency to aggregate by social phenotypes [(Jolles *et al.* 2020)](https://www.zotero.org/google-docs/?RbA8cS). Relating social phenotypes and the spatial environment within the context of multiple contagion processes (e.g., pathogen and information transmission) is another interesting frontier that can reveal how the spatial environment influences pathogen spread and socially learned behaviours simultaneously [(He *et al.* 2021)](https://www.zotero.org/google-docs/?wXyVbT).

(4) Spatial phenotype and social environment

1. *Mechanisms and consequences*

The spatial phenotypes of animals can determine the range of social environments they experience. If individuals share a spatial phenotype, they might interact and form or influence the social environment. For example, the social environment may be more expansive if home ranges are large [(Albery *et al.* 2021b)](https://www.zotero.org/google-docs/?HgNyUq) and overlapping [(Peignier *et al.* 2019)](https://www.zotero.org/google-docs/?FQe8j9). Conversely, the social environment can influence spatial phenotypes. For example, at high densities, the movements of individuals might be constrained based on competition among conspecifics, influencing their possible spatial phenotypes.

The activity budget literature represents a potential framework to integrate spatial phenotypes and the social environment, where habitat use and foraging behaviour actively shape the social environment [(Ruckstuhl 1998; Ruckstuhl & Neuhaus 2000; Pérez-Barbería *et al.* 2007)](https://www.zotero.org/google-docs/?yjiKd3). For example, animals assort into social groups based on similarities in activity budgets and dietary requirements [(Ruckstuhl & Neuhaus 2000; Bon *et al.* 2001)](https://www.zotero.org/google-docs/?wf9NNG). In addition, when the social environment changes, individuals may alter their spatial phenotypes. For example, culling badgers (*Meles meles*) disrupted their social environments, causing individuals to disperse and move further than they had previously [(Ham *et al.* 2019)](https://www.zotero.org/google-docs/?iMxi4w). In another case, hunting brown bears (*Ursus arctos*) caused surviving individuals to alter patterns of habitat selection [(Frank *et al.* 2018)](https://www.zotero.org/google-docs/?VoqxLW).

As with social phenotypes and spatial environments, the relationship between spatial phenotypes and the social environment can be considered within a behavioural reaction norm framework, describing how spatial phenotypes (e.g., movement patterns or home range size) change as a function of the social environment (e.g., group size or population density). Spatial phenotypes are often plastic because an individual’s primary response to environmental heterogeneity involves altering its space use [(Day *et al.* 2019; Schmidt & Massol 2019)](https://www.zotero.org/google-docs/?mIzmWA). A rich literature links spatial phenotypes with aspects of the social environment, such as local density. For example, positive density-dependent dispersal occurs when competition increases the likelihood of dispersing because individuals are predicted to have higher fitness at lower density sites (for a review see [(Matthysen 2005)](https://www.zotero.org/google-docs/?NIriLi)). Similarly, negative density-dependent habitat selection exists when consumer density increases and resources within preferred habitats become limited and it may be beneficial for individuals to become less selective in their habitat use (for a review see [(Avgar *et al.* 2020)](https://www.zotero.org/google-docs/?omKxV9)).

1. *Key next steps and testable hypotheses*

Linking spatial phenotypes and the social environment requires an understanding of density dependence because population density is a salient aspect of the social environment [(Matthysen 2005; Cote *et al.* 2017; Gil *et al.* 2018; Avgar *et al.* 2020)](https://www.zotero.org/google-docs/?yqar5V). For example, the **density-dependent dispersal hypothesis** [(Matthysen 2005)](https://www.zotero.org/google-docs/?ZqL7g3) predicts that individuals are more likely to leave a foraging patch or disperse when population density is high [(Cote *et al.* 2017)](https://www.zotero.org/google-docs/?PxNqvU). The expectations of density-dependent dispersal also depend on phenotypes. Some individuals are expected to be less social, to disperse at higher probability from high density environments, and to settle preferably in low density environments (Cote et al. 2017). By contrast, more social individuals may leave low density environments and settle in high density ones. Dispersal theory therefore intuitively extends to the expectations of the habitat matching hypothesis (see Section 2).

The **activity budget hypothesis** (Table 2) can help integrate spatial phenotypes and the social environment. Spatial phenotypes associated with activity budgets include movement and foraging. As animals of a similar size, sex, and age move and forage together based on their shared energetic requirements, the social environment is shaped accordingly [(Ruckstuhl 1998)](https://www.zotero.org/google-docs/?bAcobt). So far, there are few tests of hypotheses linking activity budgets with group size or composition, and then with survival or reproductive success. Additionally, activity budgets could be useful for investigating partitioning of the social environment: for example, the social environment can be simplified as either the number of competitors or number of allies in a group; when incorporating activity budgets, allies could represent group-mates with similar activity schedules, and an individual’s competitors are its group-mates with conflicting activity budgets.

### III. Shared concepts and terminology used to describe spatial and social behaviour

Our framework reveals overlap in concepts and terminology among spatial and social behaviours (Figure 1), and highlights that multiple analogous processes bridge the spatial-social interface. In Table 1, we present terms and concepts that have similarities in the study of spatial and social behaviour. Below, we highlight five examples of concepts (niche specialization, graph theory, Ideal Free Distribution and density-dependent habitat selection, Optimal Group Size theory, and Geometry of the Selfish Herd) that explicitly or implicitly bridge the spatial-social interface. We consider how each of these concepts might expand under an explicitly integrated view.

### (1) Ecological and social niche specialization

The niche is a foundational concept in the field of ecology [(Van Valen 1965; Vandermeer 1972)](https://www.zotero.org/google-docs/?KG6n99). An ecological niche comprises the environmental conditions across geographical space that a species can inhabit based on its biology and is therefore inherently a spatial feature (see Glossary). While the traditional concept of an ecological niche was meant to apply to species, individuals also occupy niches within their species’ niche, ranging from resource specialists to generalists [(Bolnick *et al.* 2003; Woo *et al.* 2008; Maldonado *et al.* 2019)](https://www.zotero.org/google-docs/?eZU2If). Individual differences in ecological niches is predicted to drive variation among individuals in fitness [(Van Valen 1965; Costa-Pereira *et al.* 2019)](https://www.zotero.org/google-docs/?nOTjhj). Social niches (see Glossary) extend the ecological niche concept by capturing the set of social environments in which a focal individual has non-zero inclusive fitness [(Bergmüller & Taborsky 2010; Montiglio *et al.* 2013; Saltz *et al.* 2016)](https://www.zotero.org/google-docs/?FZMqEr). An application of ecological niche theory to the development of social niche theory is equating an individual’s realized niche with their “social role” [(Bergmüller & Taborsky 2010)](https://www.zotero.org/google-docs/?JL4Qnn). A social role is the “*realised behaviour or tactic an individual uses in response to social challenges such as competing for food, space or mating partners*” [(Bergmüller & Taborsky 2010)](https://www.zotero.org/google-docs/?0cTDjy) and is predicted to change over time [(Montiglio *et al.* 2013)](https://www.zotero.org/google-docs/?FmS7ad). Some individuals may specialize in their social roles, whereas others may be generalists [(Pinter-Wollman *et al.* 2012)](https://www.zotero.org/google-docs/?DOJbtN). While key concepts from ecological niche theory have been applied to social niche theory [(Montiglio *et al.* 2013)](https://www.zotero.org/google-docs/?Dyxl6v), an important next step is to integrate the study of both social and ecological niches to simultaneously assess an individual’s role in the spatial and social environments.

(2) Graph theory and networks as a tool to describe social and spatial processes

Networks are often used for visualizing and analyzing interactions among biological properties, including individuals, species, or physical locations. The field of ecology has long used ecological networks to predict interactions among species [(Lusseau 2003)](https://www.zotero.org/google-docs/?d48kux). For the last two decades social networks have been used in the field of animal behaviour to study social phenotypes and environments [(Webber & Vander Wal 2019)](https://www.zotero.org/google-docs/?3FFRTZ). Social networks depict individual animals as nodes and pairwise interactions or associations between individuals as edges [(Croft *et al.* 2008)](https://www.zotero.org/google-docs/?N1CITb); ecological networks typically depict species as nodes, while edges are species interactions such as host-parasitoid, plant-pollinator, predator-prey, or spatial co-occurrence [(Ings *et al.* 2009)](https://www.zotero.org/google-docs/?WoRVzB). Meanwhile, ‘movement networks’ describe animals’ movements with discrete physical locations as nodes and animal movements between the locations as edges [(Mourier *et al.* 2019)](https://www.zotero.org/google-docs/?SHUpL9). Spatial networks represent features of the spatial environment, including habitats or resource patches [(Silk *et al.* 2018b; Bastille-Rousseau *et al.* 2020; He *et al.* 2021)](https://www.zotero.org/google-docs/?6tYOB2). Despite their similarities and common reliance on graph theory, social, ecological, movement, and spatial networks are largely applied distinctly from one another.

Recently, multilayer networks [(Kivela *et al.* 2014)](https://www.zotero.org/google-docs/?AGTBak) have been proposed as a novel analytic tool to examine multiple layers of spatial and social processes, presenting both methodological and conceptual advances over prior methods [(Silk *et al.* 2018b)](https://www.zotero.org/google-docs/?GI6E3B). For example, partitioning spatial or social behaviours across network layers may enable fine-scale assessment of behaviours’ context dependence [(Barrett *et al.* 2012; Finn *et al.* 2019)](https://www.zotero.org/google-docs/?vs3ZKv). A multilayer network framework further allows the integration of species interactions across different ecological situations, such as different locations or habitats [(Pilosof *et al.* 2017)](https://www.zotero.org/google-docs/?kjXbMc). Future work could apply multilayer networks to integrate the spatial-social interface with ecological theory by linking social, ecological and spatial networks in a unified framework. For example, networks describing the social structure of predator and prey species could be linked in a multilayer network to test hypotheses about how social processes at one trophic level might influence social patterns at another. In this example, the implicit aspects of social network analysis (i.e., interactions or associations among members of the same species) are integrated with inherent aspects of ecological networks (e.g., predators-prey dynamics) and would require that processes that are being examined at social and ecological levels occur on a similar timescale [(Montiglio *et al.* 2020)](https://www.zotero.org/google-docs/?6teLiE). Multilayer networks could be useful to describe how social and spatial phenotypes influence contact processes and thereby pathogen transmission [(Albery *et al.* 2021a; Silk & Fefferman 2021)](https://www.zotero.org/google-docs/?q7DLUj). For example, [Silk *et al.* (2018a)](https://www.zotero.org/google-docs/?2M8LMA) used multi-layer networks to link badger-cow interactions with a spatial network of the badgers’ latrines to study the transmission of bovine tuberculosis. Multi-host multi-pathogen networks represent a more complicated variation on this theme [(Fountain-Jones *et al.* 2018)](https://www.zotero.org/google-docs/?IvxgPV).

(3) Ideal Free Distribution and density-dependent habitat selection

Classic habitat selection theory is based on the Ideal Free Distribution (IFD), which posits that habitat selection is density-dependent and variation in density between habitats leads to a fitness equilibrium [(Fretwell & Lucas 1969; Bradbury *et al.* 2015)](https://www.zotero.org/google-docs/?sZMK1s). The available resources within a habitat sustain a certain number of individuals and in a finite world, fitness in a habitat is predicted to decline as a function of density [(Morris 1987, 2011)](https://www.zotero.org/google-docs/?gFIRpO). Consumers are predicted to aggregate in high quality habitats, but space apart to reduce competition [(Sutherland 1983)](https://www.zotero.org/google-docs/?kJI23V). While the IFD explicitly predicts that animals should assort in space to equalize fitness, the Ideal Despotic Distribution (IDD) predicts heterogeneous fitness due to dominant individuals forcing others into lower quality habitats [(Oro 2008)](https://www.zotero.org/google-docs/?fqTBO6). The IDD often occurs in territorial systems where habitat selection of subordinate individuals is constrained by territoriality of dominant individuals [(Oro 2008)](https://www.zotero.org/google-docs/?2mBSgt). While the IFD and IDD implicitly incorporate social processes, there has been little *explicit* consideration of the social processes underpinning the IFD and IDD. Many exciting opportunities exist to quantify the role of social phenotypes and the social environment within these foundational ecological concepts to help shed light on the mechanisms that influence the distribution of animals in space.

(4) Optimal group size

Optimal group size theory posits that group size is shaped by balancing the costs (e.g., competition) and benefits (e.g., protection from predation) of group living [(Sibly 1983; Fryxell *et al.* 2007)](https://www.zotero.org/google-docs/?4TY0bz). Optimal group size theory explicitly addresses group size (i.e., the social environment) while the underlying spatial processes are implicit. Nevertheless, the spatial environment plays a key role determining group size. For example, group size-fitness optima depend on resource availability and predation risk in the habitat [(Webber & Vander Wal 2018)](https://www.zotero.org/google-docs/?PgtvXk). As highlighted in Section II, the social and spatial environments are often correlated and living in a group may be beneficial only in certain environmental conditions. Animals are therefore predicted to balance the costs and benefits of grouping as a function of the spatial environment and form groups of optimal size where fitness is maximized [(Higashi & Yamamura 1993)](https://www.zotero.org/google-docs/?nCCCcb). Species with fission-fusion dynamics offer a unique opportunity to study the relationship between optimal group size and the spatial environment.

(5) Geometry of the selfish herd

The geometry of the selfish herd (GSH) describes the spatial arrangement of gregarious animals in response to predation risk [(Hamilton 1971)](https://www.zotero.org/google-docs/?vfLBoY). An important benefit of group living is the reduced *per capita* cost of predation, i.e., the detection-dilution trade-off [(Krause & Ruxton 2002)](https://www.zotero.org/google-docs/?dxM3tV). However, the geometry of the selfish herd suggests that risk is not equal among individuals in a group. Although the concept was initially formulated based on an undetected predator randomly appearing at any location within a group of prey and attacking the nearest individual [(Hamilton 1971)](https://www.zotero.org/google-docs/?TdBlDU), the domain of danger (i.e., the area around an individual in which it is exposed to predation) is often smallest at the group’s centre, in which case individuals should seek to position themselves in both spatially and socially central positions to minimize their risk of predation and maximize fitness [(Morrell *et al.* 2011; Dostie *et al.* 2016; Bonar *et al.* 2020)](https://www.zotero.org/google-docs/?FexkSO). For example, sheep move towards the centre of the herd when herded by dogs [(King *et al.* 2012)](https://www.zotero.org/google-docs/?oifaTC), and redshanks (*Tringa totanus*) at the edge of their flock are targeted by sparrowhawks (*Accipiter nisus*) [(Quinn & Cresswell 2006)](https://www.zotero.org/google-docs/?P4XPTQ). The GSH provides an explicit integration of theory from social and spatial behavioural ecology that remains to be explored within our proposed spatial-social interface framework. Specifically, the GSH inherently relies on variation in risk within the spatial environment; for an individual to alter their domain of danger, they may change both social and spatial phenotypes, e.g., by becoming more central spatially or socially. Other forms of threat (e.g., from infectious pathogens) may offer countervailing selective pressures by reducing fitness of individuals with high social and/or spatial centrality [(Ferrari *et al.* 2006)](https://www.zotero.org/google-docs/?oblhxS).

## IV. Movement as a mechanism for linking social and spatial behaviour

To consider the causes and consequences of social interactions within a spatial context we suggest that movement ecology [(Nathan *et al.* 2008)](https://www.zotero.org/google-docs/?ppjJCA) presents a useful conceptual tool with which to interrogate the spatial-social interface (Figure 2). Mapping the spatial-social interface to specific aspects of movement ecology clarifies how hypotheses surrounding the spatial-social interface can be empirically tested (Figure 2). Movement ecology integrates the causes and consequences of movement vis-a-vis the ecology and evolution of individuals or populations [(Nathan *et al.* 2008)](https://www.zotero.org/google-docs/?GVt79I). Patterns of animal movement both drive and emerge from individual decisions at the spatial-social interface. The causes and consequences of movement differ among individuals and across a range of ecological contexts [(Shaw 2020)](https://www.zotero.org/google-docs/?3Pwsah), and it is increasingly clear that animal movements affect and mediate the relationship between spatial and social processes. The movement ecology paradigm is composed of three factors related to an individual – internal state, motion capacity, and navigation capacity – as well as a fourth component related to external factors – the social or spatial environment – affecting movement [(Nathan *et al.* 2008)](https://www.zotero.org/google-docs/?NUDHPp). In this section, we highlight the relationship between these factors and the spatial-social interface.

1. Internal state

The internal state accounts for the physiological and psychological state of the focal individual and asks and answers the question: ‘‘*why move?*” [(Nathan *et al.* 2008)](https://www.zotero.org/google-docs/?0Tqg6L). Animals move to locate and acquire sustenance (i.e., food and water), which is influenced by a metabolic clock and requires maintenance throughout an individual’s lifetime (though metabolic maintenance can be passive, as in the case of some thermal, chemical, or salinity requirements). Animals further move to follow resources (e.g, migration) and gain new breeding opportunities (e.g., dispersal). When considering *why* animals move, both social and spatial environments must be considered at proximate and ultimate levels. For example, an individual’s internal state can drive movement to, or from, resources that satisfy metabolic (e.g., hunger) or social (e.g., affiliative relationships) requirements. Consequently, the spatial and social environment an individual experiences emerges from patterns of movement and the distribution of resources needed to satisfy internal requirements (e.g., food or social partners). Another aspect of an animal’s internal state that can influence why an individual moves is among individual differences in behaviour, or animal personality, including spatial personalities [(Spiegel *et al.* 2017; Stuber *et al.* 2022)](https://www.zotero.org/google-docs/?oi7gPz).

Fission-fusion social dynamics, where groups merge and split overtime, represent a poignant example of movement at the spatial-social interface that can be attributed to internal state. For example, competition for food often motivates groups to separate (i.e., fission) and move away from each other during foraging [(Jacobs 2010)](https://www.zotero.org/google-docs/?D6AjJf). In this case, the interaction between the social environment (i.e., competition) and spatial environment (i.e., availability of food) answers the question “*why move?*”. Moreover, the adaptive value of fission-fusion lies in the ability for groups to balance the costs and benefits of social grouping, i.e., fission to avoid competition during foraging and fusion to improve information transfer and reduce risk of predation – factors that satisfy internal requirements [(Sueur *et al.* 2011)](https://www.zotero.org/google-docs/?9H4f6b). Similarly, dispersal movements within populations can be generally attributed to characteristics of the social (e.g., local density or group size) and spatial (e.g,. habitat characteristics) environments; however, dispersal propensity can differ between individuals in the same population [(Delgado *et al.* 2010)](https://www.zotero.org/google-docs/?umZszT). One explanation for individual differences in dispersal propensity is phenotype-dependent dispersal, which is related to internal state and means that dispersal is correlated with phenotypic traits [(Clobert *et al.* 2009)](https://www.zotero.org/google-docs/?HkMmVJ). For example, social personality is correlated with post-dispersal settlement decisions in lizards (*Lacerta vivipara*), such that more socially tolerant lizards settle in high density habitat patches [(Cote & Clobert 2007)](https://www.zotero.org/google-docs/?U7oIgT). Investigating an individual’s internal state and asking *why* animals move provides an opportunity to test mechanisms that drive the spatial-social interface.

1. Motion capacity

An individual’s motion capacity accounts for its ability to move and asks and answers the question: “*How to move?*” [(Nathan *et al.* 2008)](https://www.zotero.org/google-docs/?PFirwj). At its core, motion capacity is an organism’s biomechanical and physiological ability to move. Although fixed for most species, motion capacity can still depend on the spatial-social interface. For example, movement capacity can be restricted by both the spatial environment (e.g., deep snow: [Pedersen *et al.* 2021)](https://www.zotero.org/google-docs/?oDfkms), and social environment (e.g., active defense of a territory: [Heap *et al.* 2012)](https://www.zotero.org/google-docs/?xm8HE0). Territoriality represents a unique integration of motion capacity within the spatial-social interface. Specifically, territory boundaries have social and spatial barriers within which territorial animals live and these barriers define how animals move. For highly social territorial species, the social contacts of a focal individual could be limited only those individuals that share the same or neighbouring territories [(Brandell *et al.* 2021)](https://www.zotero.org/google-docs/?Sum0KQ), whereas for less social territorial species, social contacts may extend only to individuals with adjacent territories or competitors attempting to usurp their territory [(Spiegel *et al.* 2018)](https://www.zotero.org/google-docs/?phFH48). Motion capacity could also incorporate an individual’s capacity to move long distances. For migratory animals, social barriers associated with information transfer during migration can drive how individuals obtain cues about the environment, and therefore how they move, with potential to promote the evolution of collective migration [(Guttal & Couzin 2010)](https://www.zotero.org/google-docs/?G1piSZ). In addition, individuals with greater movement capacity will have larger home ranges and may therefore have more social contacts [(Albery *et al.* 2021b)](https://www.zotero.org/google-docs/?Ru9Nb5) and engage in mating events more frequently [(Pollo *et al.* 2021)](https://www.zotero.org/google-docs/?X4H5z5). We posit that aspects of the spatial-social interface, e.g., deep snow in the spatial environment or social barriers in the social environment, can promote or inhibit *how* animals move within certain contexts.

1. Navigational capacity

Navigational capacity accounts for the ability of an individual to orient in space and/or time and addresses the question: ‘‘*when and where to move?*’’ [(Nathan *et al.* 2008)](https://www.zotero.org/google-docs/?LVBDRe). An individual’s movements are often guided by when and where the individual can pursue a goal – for example, move towards food or away from a threat. Importantly, navigation requires an ability to sense and respond to information about the spatial *and* social environments. When navigating, animals inevitably rely on the integration of spatial and social information to decide *when and* *where to move.* For example, individuals moving in high density populations can directly influence one another [(Reynolds 1987; Couzin *et al.* 2002)](https://www.zotero.org/google-docs/?OvwEOH).

These influences — called interaction rules (Couzin *et al.* 2002) — can underpin a range of beneficial emergent properties of groups. For example, schools of fish are better at detecting shaded (preferred) versus unshaded (less preferred) microhabitats than single fish, a process also known as “collective sensing” [(Berdahl *et al.* 2013)](https://www.zotero.org/google-docs/?VUxHIB). Groups can also benefit from information pooling, where the average of many noisy estimates captures an accurate estimation. For example, if each individual in a group approximates the direction to a resource with some error, the average of these estimates can be relatively error-free, i.e., the “many wrongs” principle [(Simons 2004)](https://www.zotero.org/google-docs/?cgYXQi). Interaction history can also shape when and where to move, with more socially connected individuals potentially having more [(Strandburg-Peshkin *et al.* 2018)](https://www.zotero.org/google-docs/?ETcGXs) or less influence [(Papageorgiou & Farine 2020b)](https://www.zotero.org/google-docs/?pVok5z). As a result, what components of the environment that individuals experience can be largely driven by social phenotypes. Moreover, social phenotypes that dictate leader-follower dynamics may emerge and could influence the navigational capacity of individuals or groups [(Couzin *et al.* 2005)](https://www.zotero.org/google-docs/?NDrn8t). Travel routes for navigating birds can also be influenced by the spatial-social interface. For example, group size is predicted to increase to an optimum size such that accurate navigation is guaranteed, groups smaller than the optima should either have better navigational tools than larger ones or should suffer greater losses during movement [(Conradt & Roper 2005)](https://www.zotero.org/google-docs/?G4vS7c). Navigational capacity and the questions of *when and where* to move are key mechanisms when considering the spatial-social interface.

## V. Conclusion

The spatial-social interface emerges from the interactions between social and spatial phenotypes and environments. Our framework conceptualizes these interactions by highlighting theoretical and empirical links between components of the spatial-social interface and by proposing new questions and testable hypotheses within the context of each pairwise interaction at the interface (Figure 1; Table 2). We propose the spatial-social interface as a conceptual framework and a roadmap for future studies to integrate social and spatial behaviour, while situating the interface in the context of existing theory and empirical examples. Our framework relies on understanding social and spatial aspects of an animal’s life, integrating these aspects and their interactions, and conceptualizing these interactions within the context of individual fitness and population dynamics. We also introduce the idea that movement ecology could be a key mechanism bridging the spatial-social interface in that spatial and social phenotypes almost always require movement to, from, or within the spatial and social environments. Although the questions of *why, how, when, and where to move* were first proposed to explain movement ecology, there is a natural extension between the spatial-social interface and the movement ecology paradigm. We hope our synthesis and framework helps integrate these often-disparate subdisciplines and that future work will begin to share common vocabulary, theory, and methods to motivate broad impactful advances.

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**Figure 1.** Conceptual symmetry at the spatial-social interface, decomposed into 1) spatial *versus* social environment; 2) spatial *versus* social phenotype; 3) spatial environment *versus* social phenotype; 4) social environment *versus* spatial phenotype. Numbers for each pairwise interaction correspond to the detailed overviews of each interaction in Section II. Social phenotypes emerge from interactions among individuals, including social centrality, number of mates, and dominance rank, while the social environment comprises aggregative attributes of individuals, including group size, population density, and meta-population structure. Similarly, spatial phenotypes comprise movement behaviours to, from, and within geographic and environmental space, including home range size, habitat preference, and movement patterns, while the spatial environment incorporates aspects of geographic and environmental space, including habitat configuration and the landscape of fear. The social phenotype-social environment and spatial phenotype-spatial environment arrows are gray as these domains are well covered in existing literature and conceptual frameworks.



**Figure 2.** Movement ecology as a mechanism that mediates the spatial-social interface. Aspects of the spatial environment (e.g., habitat, box a) and social environment (e.g., social groups, box b) are related to one another through feedbacks, but they also affect an individual’s internal state (box c) as well as spatial (box d) and social navigational capacities (box e). For example, the caloric intake an animal gains from a particular foraging patch in the spatial environment (box a) may depend on how many group mates it has who can help subsidize vigilance for predators (box b). Whether an animal should move to an alternative patch might therefore depend on how hungry it is (its internal state, box c) and how much it can satisfy that hunger in the spatial and social environments the new patch provides. Regardless of where the individual should move to optimize its caloric intake, where it actually moves will depend on both its spatial and its social navigational capabilities, e.g., can the animal identify a prospective patch as offering high quantity or quality calories (box d) and can it identify a set of conspecifics to effectively or ineffectively subsidizing vigilance (box e). Together, the spatial and social navigational capacity of an individual are mechanisms that influence movement behaviour, which in turn has potential to enter a feedback loop. Within the feedback loop, individual movement can affect, and can be affected by, spatial (box g) and social phenotypes (box h), which in turn can affect, and can be affected by, collective movement (box i). Finally, the feedback between individual movement ↔ spatial phenotypes ↔ social phenotypes ↔ collective movement leads to population-level space use (box j) and population-level social structure (box k). Individual movement is positioned at the centre of the spatial-social interface and represents the connection between social and spatial environments (top half of the figure) and social and spatial phenotypes (bottom half of the figure).

**Table 1.** Concepts that appear in studies of both spatial and social behaviour.

|  |  |  |  |
| --- | --- | --- | --- |
| **Spatial concept** | **Definition** | **Social concept** | **Definition** |
| Spatial environment | The geographic and environmental space (see Glossary). More specifically, the abiotic and biotic patterns of risks, resources, and climatic conditions through space and time that animals interact with. | Social environment | The conspecifics that an individual interacts with. More specifically, group size and composition, and the social interactions in various social situations (e.g., affiliative, agonistic) among individuals within a group or population. |
| Spatial phenotype | The space use of an individual (e.g., an individual's home range, movement patterns, refuge site). | Social phenotype | The social position of an individual in a society that emerges from its social interactions (e.g., mating, grooming etc.) with other individuals.  |
| Ecological niche | A spatial distribution that is constrained based on the biophysical and environmental conditions across geographical space that permit an individual to survive and reproduce. Niche variation is predicted to affect fitness variation. | Social niche | A set of social interactions, which are constrained by the social environments. According to the definition by Saltz et al. (2016), a focal individual can have non-zero inclusive fitness in their social niche [(Saltz *et al.* 2016)](https://www.zotero.org/google-docs/?TJTqmt). |
| Spatial connectivity | Structural configuration of landscape features that allows or restricts animal movement between locations. For example, rivers, lakes, or mountain ranges may facilitate or restrict spatial connectivity among individuals. | Social connectivity | The frequency or tendency for animals in a population to interact or associate with one another. The structural configuration of social connections allows or restricts individuals from interacting. For example, competition or affiliative interactions may facilitate or restrict social connectivity among individuals. |
| Spatial density  | The potential for a phenotype of species, population, or individual to change as a function of changes in *population density*. Population density is typically defined as the number of animals in a given area, measured, for example, as the intensity of a Poisson point process of animal occurrences over space.  | Social density | The number and strength of social interactions among individuals within a given area; can be operationalized as graph density.  |

**Table 2:** Summary of hypotheses presented in Section II.

|  |  |  |  |
| --- | --- | --- | --- |
| **Section** | **Hypothesis** | **Prediction(s)** | **Key references** |
| (1) social environment and spatial environment | Social resistance hypothesis | Genetic relatedness and gene flow could be influenced by the relationship between the social and spatial environments.  | [(Armansin *et al.* 2020)](https://www.zotero.org/google-docs/?wbVhg3) |
| Environmental engineering hypothesis | The social environment of animals that build their own shelter (e.g., dens, nests, or burrows) can influence the structure of the spatial environment. For example, nests of social insects, beaver dams, or spider webs. | [(Doody *et al.* 2021)](https://www.zotero.org/google-docs/?0DMo9Y) |
| (2) social phenotype and spatial phenotype | Pace-of-life syndrome hypothesis  | Physiology (e.g., hormone production) or life-history (e.g., senescence) may shape variation in spatial and social phenotypes. Specific predictions linking physiology and life-history with spatial and social phenotypes are widespread. | [(Silk & Hodgson 2021)](https://www.zotero.org/google-docs/?1Xm7QM) |
| Habitat matching hypothesis | Population density may relate to settlement decisions with less social individuals settling in lower density patches, which may have lower quality resources. Foraging in low quality habitats requires individuals to move more to encounter resources, therefore resulting in covariance between spatial and social phenotypes with less social individuals moving more than more social individuals.  | [(Fagen 1987; Morris 1994)](https://www.zotero.org/google-docs/?6Wlfg2) |
| (3) social phenotype and spatial environment | Social reaction norm hypothesis | The spatial environment is composed of both dynamic (e.g., predator presence) and static (e.g., local topography) components. Social phenotypes may change in response to the dynamic components of the spatial environment and changes might happen at different temporal scales, which relate to the rate of change in the spatial environment. | [(Martin & Jaeggi 2021; Strickland *et al.* 2021)](https://www.zotero.org/google-docs/?wWomsS) |
| Information centre hypothesis | Social living is advantageous because individuals may acquire information about resources by following cues from informed individuals at shared locations, such as roosts or nests, and follow informed individuals to new resources. | [(Ward & Zahavi 1973; Harel *et al.* 2017)](https://www.zotero.org/google-docs/?XPue2l) |
| (4) spatial phenotype and social environment | Density-dependent dispersal hypothesis  | Individuals are more likely to leave a foraging patch or disperse when population density is high. | [(Matthysen 2005; Cote *et al.* 2017)](https://www.zotero.org/google-docs/?OG9L1R) |
| Activity budget hypothesis | Given the social environment can be simplified as either the number of competitors or number of allies in a group, the proportion of competitors (individuals of differing size) or allies (individuals of similar size) is predicted to influence spatial phenotypes (e.g., movement or foraging behaviour). | [(Ruckstuhl 1998)](https://www.zotero.org/google-docs/?CSGhpT) |

**Glossary of key terms.**

|  |  |
| --- | --- |
| **Term** | **Definition** |
| Animal personality or behavioural type | Consistent differences in behaviour among individuals over space or time [(Sih *et al.* 2004)](https://www.zotero.org/google-docs/?wU8mXb).  |
| Behavioural syndrome | Covariation, or correlations, between consistent among-individual differences in behaviour over time and/or across situations [(Sih *et al.* 2004)](https://www.zotero.org/google-docs/?b2Usyr). |
| Behavioural reaction norm | The behavioural phenotypes that a single individual produces over a set of environments [(Dingemanse *et al.* 2010)](https://www.zotero.org/google-docs/?9JwCtM). |
| Environment | Set of spatial or social elements that an animal faces (see below for definitions of spatial and social environments). |
| Environmental space | The conditions (e.g., temperature or humidity), risks (e.g., predators), and resources (e.g., food) and their spatial distributions within which an individual exists [(Matthiopoulos *et al.* 2020)](https://www.zotero.org/google-docs/?jJz8dU). |
| Geographic space | The position, size, shape, and location of home ranges and the physical attributes within the range of an animal [(Moorcroft 2012)](https://www.zotero.org/google-docs/?OaMJVm). |
| Phenotype | Suite of measurable and consistent characteristics that emerge from interactions between an individual’s genotype and its environment. |
| Spatial proximity | Adjacency of individuals in space, which can be measured as Euclidean distance. |
| Social association | Animals’ tendency to be in spatial proximity; usually a prerequisite for social interaction [(Ginsberg & Young 1992)](https://www.zotero.org/google-docs/?Xy4v5f). |
| Social environment | The size and composition of a group and the type of interactions (e.g,. affiliative, agonistic, etc) among individuals within a group or population [(Farine 2015)](https://www.zotero.org/google-docs/?NziNrX). |
| Social phenotype | The social position of an individual in a society that emerges from its social interactions (e.g., mating, grooming etc.) with other individuals.  |
| Spatial environment | The environment that concerns both geographic and environmental space. |
| Spatial phenotype | The space use of an individual (e.g., an individual's home range, movement patterns, refuge site). |

##

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